13.

Ocular Anatomy and Light Sensitivity Studies on the Blind Fish from Cueva de los Sabinos, Mexico.

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(Plate I; Text-figures 1-3).

Introduction.

The discovery of another blind characin from the Mexican caves of the State of San Luis Potosi, which is advanced beyond the conditions of eye degeneration found in the specimens of La Cueva Chica, calls for an examination of this new form in regard to its ocular anatomy and reactions to light. The present contribution is thus a continuation of the studies of Gresser & Breder (1940) and Breder & Gresser (1941a, b and c).

The finding of this fish, under taxonomic study by Dr. C. L. Hubbs, has been reported by Tafall (1942 and 1943). This second cave, Cueva de los Sabinos, is about fifteen miles distant from La Cueva Chica. Chemitropic reactions of this fish, the La Cueva Chica specimens and the deriving river fish, *Astyanax mexicanus* (Philippi), have been reported by Breder & Rasquin (1943). The current status of the whole problem and a preliminary notice of some of the conclusions of the present paper have been given by Breder (1943c).

The experimental part of the study has been carried on in the Department of Animal Behavior of the American Museum of Natural History. The histological sections of the head have been made by Miss Priscilla Rasquin. The cleared and stained skulls have been prepared by Miss A. M. Holz. Dr. Ralph Meader, of Yale University, examined and interpreted certain of the sections and provided the photographs of Plate I. Dr. W. K. Gregory gave advice in connection with interpretation of the osteological changes. Dr. E. B. Gresser, of New York University, gave helpful aid in connection with the comparisons of the ocular details. To all of these people the author wishes to express his grateful appreciation.

Structure of the Eye.

Compared with the eye remnant of the fishes from La Cueva Chica, described by Gresser & Breder (1940) and Breder & Gresser (1941a), the optical architecture of the fishes from Cueva de los Sabinos is still further reduced. Hardly anything is left of the eye capsule found in the more advanced of the mixed fishes from La Cueva Chica. In addition to this great reduction of the capsule there is no optic nerve connecting with the brain.

Unsatisfied with the difficulties in finding and interpreting these remnant structures, the slides were referred to Dr. Ralph Meader of Yale University who is engaged in studying the brain tracts of these fishes. His careful examination of the slides brought out numerous fine details about which he wrote as follows, for inclusion in this paper.

"An optic capsule is present embedded in the fat which fills the region of the head normally occupied by the eye and orbit in eyed river fish. The capsule consists of a sphere of moderately heavy cartilage, incomplete on its medial wall where it is replaced by a lamina of dense connective tissue. Within the capsule is a more or less loose network of connective tissue in which lies a small heavily pigmented sphere or cyst, which presumably represents the choroid coat. Although some stainable material is visible within this cyst and it contains some cells of unidentified origin, no recognizable elements of a retina can be found. There is no lens nor any of its associated structures. Outside of the pigmented sphere are a few vascular channels which are probably the remnant of the choroidal gland. A few strands of striated muscle are seen in the region of the connective tissue which completes the medial wall of the cartilaginous outer layer of the capsule. The muscle fibers do not show well the normal histology of voluntary muscle. Near them, attached to one capsule, can be seen a small bundle of tissue which in its shape and position resembles the atrophic optic nerves of some blind specimens from La Cueva Chica. The bundle can be traced medialward only a short distance from the capsule before it becomes very small and then ends. No similar bundle can be seen attached to the other capsule.

"From the anterolateral aspect of each optic capsule a stalk of tissue extends towards the skin. On one side this stalk is small and hollow near the capsule. A few cells with large nuclei line the cavity which is filled with amorphous débris. Nearer the skin the stalk becomes smaller and solid. Its final attachment cannot be certainly made out because of torn sections, but it probably attaches to the connective tissue underlying the skin that covers over the obliterated orbital cavity. On the opposite side of the head, the stalk is relatively large, hollow, and has definite attachment to the skin. The same type of cells with large nuclei lines its cavity and the cells which form the rest of its thick wall resemble somewhat those of the skin. At one place they nearly become continuous with the surface epithelium. These stalks resemble those described by Gresser & Breder (1940) and Breder & Gresser (1941a) for the blind fish from La Cueva Chica. They are most like that shown in their figure 2 (1941a).

"The condition of this optic capsule in the Sabinos fish seems to be an exaggeration of the reduction in size and in the loss of retina seen in occasional specimens from La Cueva Chica. For example one of the latter specimens prepared here exhibits no retinal structure although in one pigmented cyst is evident a multipolar nerve cell whose presence I cannot explain. This specimen, however, does have an optic nerve that can be traced to the brain whereas in the Sabinos specimen, no optic nerve can be certainly identified and the strand tentatively named the optic nerve peters out in the orbital fat. No optic nerve can be found connected with the brain."

Plate I shows sections illustrating the above description and is comparable to the plates in Breder & Gresser (1941a) of the La Cueva Chica material, and taken together they clearly indicate the increasing reduction of architectural detail.

Modifications of the Skull.

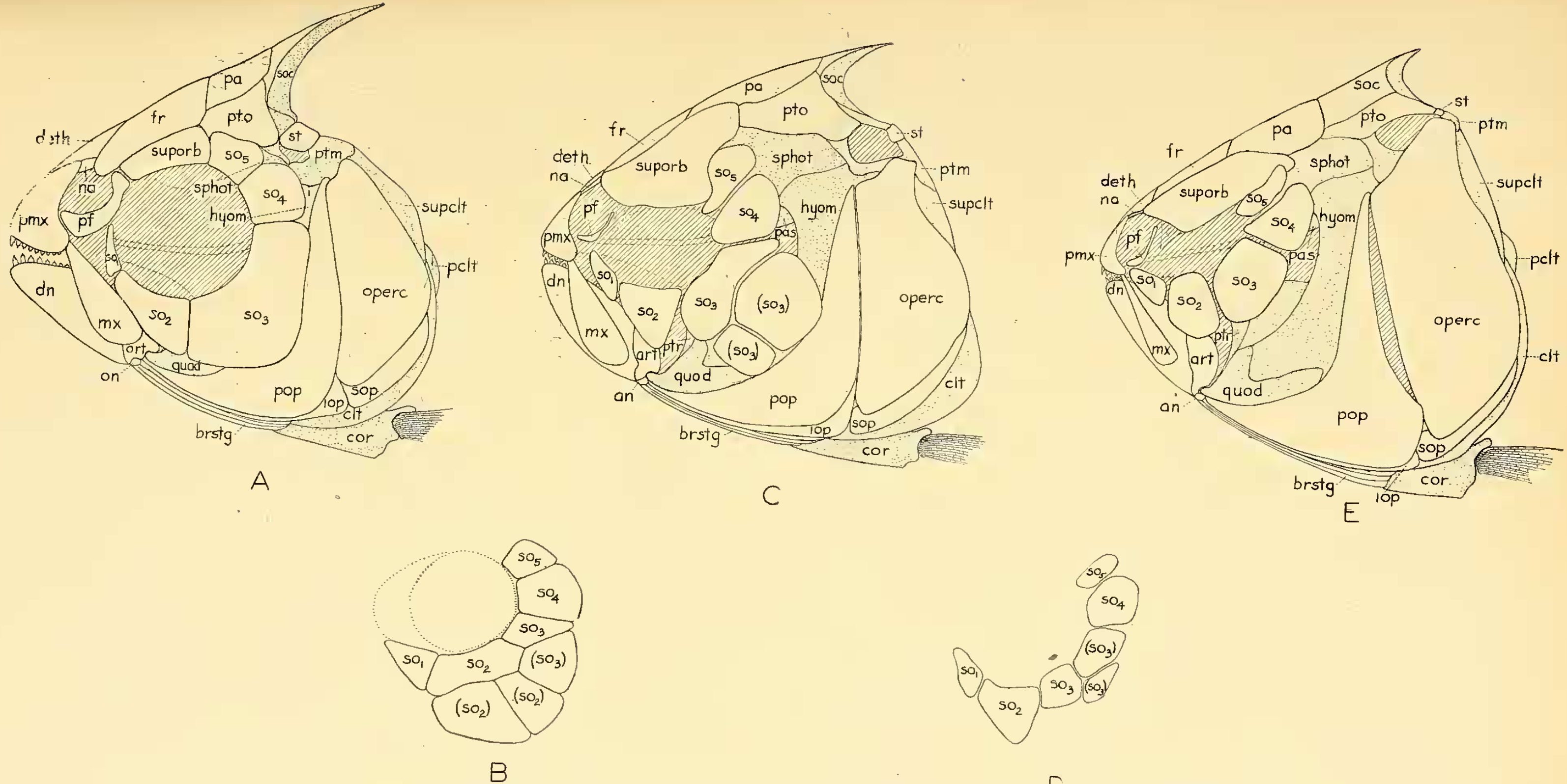
With such a reduction of the eye it is to be expected that the osteological elements surrounding this area should show some modification. These include progressive changes accompanying the reduction of the globe and involve conspicuously a closing in of the circumorbital series of bones. The details of these changes in the conformation of the skull are indicated in Text-figure 1, which has been based on camera lucida drawings of cleared and stained heads. The sutures in the outer series of bones were easily evident, but some of the elements of the chondrocranium were discerned with difficulty or not at all, leading to the omission of certain bone names in the figure.

The normal-eyed river fish, Text-figure 1a, shows a series of five suborbital bones and a well ossified skull, as was evidenced by the taking of the stain (alizarin). This skull is a generalized type of characin skull as may be noted by a comparison with the figures of Gregory (1933) and Gregory & Conrad (1938). It resembles clearly that of *Cheirodon*, which these authors, following Eigenmann (1917), consider basic to the group containing *Astyanax* and which they designate the Cheirodontinae.

A specimen from La Cuevva Chica with a reduced eye shows an essentially similar structure, but with the circumorbital series of bones closed in and with the addition of three new elements. These are evidently fragmentations of so_2 and so_3, or new centers of ossification induced primarily by the shrinkage of the eye diameter. The arrangement of this series of bones is indicated in Text-figure 1b, together with the diameter of the globe and the larger anterior extension of the orbit.

A typical blind fish from La Cueva Chica shows a still further closing in of the suborbital series, with the elimination of the globe proper, Text-figure 1c, and what appears to be a fragmentation of so_3 into three elements. This is one less than the number of new elements shown by the fish with merely a reduced eye diameter, and there are other changes to be discussed later. A second specimen of the same type showed a similar fragmentation of this bone, but the arrangement of the separate elements is rather different. This series of circumorbital bones is seen in Text-figure 1d. Both these fishes showed minor variations in these details from side to side. Such variations in the mixed fishes from La Cueva Chica should probably be expected in any structure associated with the features of reduction and are evidently equivalent to the variations in the eye itself already discussed by Breder & Gresser (1941a).

A specimen from Cueva de los Sabinos shows a still further closing in of the suborbital series, as is indicated in Text-figure 1e. Along with this but not indicated in the figure is an evident reduction of ossification, indicated by the manner in which the stain is retained. It will be noted that the circumobital series has returned to five in number; thus the fragmen-



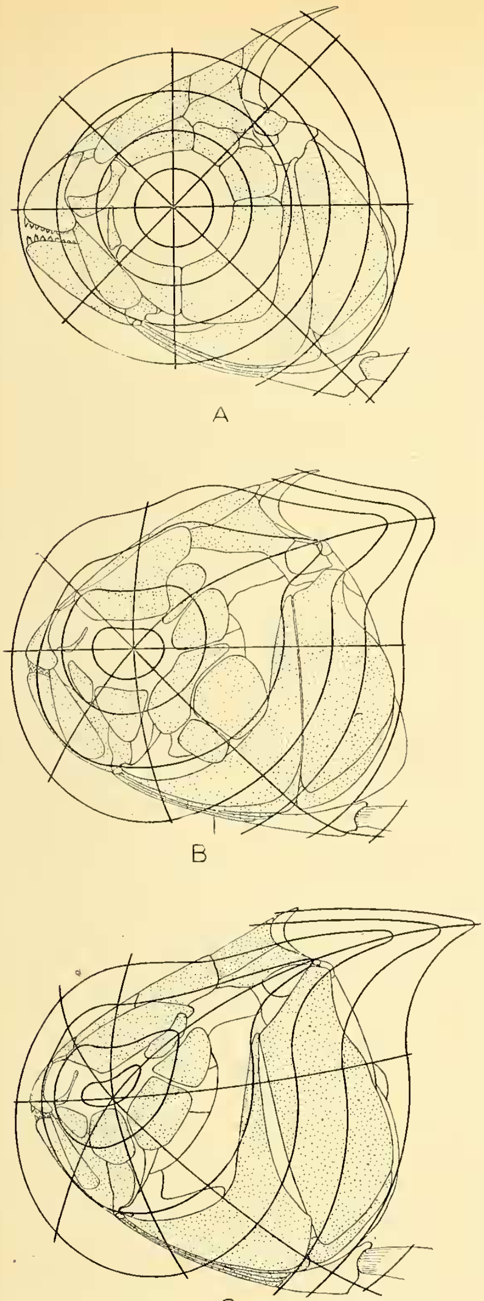
TEXT-FIG. 1. Skulls of cave fish series. **A.** Normal-eyed river fish. **B.** Circumorbital bones of perfect but small eyed specimen. The dotted lines indicate the outline of the orbit and the globe of the eye. **C.** Fully blind specimen from La Cueva Chica. **D.** Circumorbital bones of another fully blind specimen from La Cueva Chica. **E.** Cueva de los Sabinos fish. Abbreviations: **an**—angular, **art**—articular, **brstg**—branchiostegal, **clt**—cleithrum, **cor**—coracoid, **deth**—dermethmoid, **dn**—dentary, **fr**—frontal, **iop**—interopercular, **mx**—maxilla, **na**—nasal, **operc**—opercular, **pa**—parietal, **pas**—parasphenoid, **pclt**—postcleithrum, **pf**—prefrontal, **pmx**—premaxilla, **pop**—preopercular, **ptm**—posttemporal, **pto**—pterotic, **ptr**—pterygoid, **quad**—quadrate, **so**—suborbital, **soc**—supraoccipital, **sop**—subopercular, **sphot**—sphenotic, **st**—supratemporal (scale bone), **supclt**—supracleithrum, **suporb**—supraorbital.

tation or new elements, is evidently a transient phenomenon, which reaches its highest development immediately on the reduction of the eye size and is then gradually reduced to the original state, perhaps as a new level of organizational stability is attained. This specimen, on the other side, was not so far reduced, so_3 being represented by two elements which occupy an area nearly equivalent to that of the single so_3 on the side illustrated.

The increased exposure of the chondrocranial elements is evident from the series of three skulls in Text-figure 1, as the surface bones crowd forward as the eye is reduced. If there is any involvement of the basic nature of the jaw musculature, as found by Petit (1940) for *Typhleotris madagascariensis* Petit and *Coecobarbus geertsi* Boulenger, it is not evident from these specimens. Text-figure 1 well indicates the reduction of the size of the maxilla, premaxilla and dentary and the near loss of the prefrontal. Otherwise there is a general shifting around of all the head bones in more or less minor fashion, as they evidently spread or contract to fit the new conditions imposed by the removal of the eye. The greatly increased size of the supraorbital is notable. The sclerotic bones, not illustrated, are normal and ossified in the river fish but they degenerate and disappear along with the globe, except as they are possibly represented by some small cartilaginous remnants. The curious backward extension of the angle of the properculum in the Cueva de los Sabinos fish and its median separation from the operculum were hardly to be expected. The pointed posterior process of the supraoccipital is reduced in size materially in this series, moving forward as it and the parietal usurp the place occupied by the reducing frontal on the top of the skull.

The above-mentioned changes are hard to comprehend and give the impression of being hit-or-miss and that they might just as well have taken on a variety of other arrangements. On analysis it is seen, however, that actually there is a large amount of regularity in these transforming skulls and that the osteological elements are moving and rearranging themselves under the force of some general regulating control. This may be most readily visualized if we make use of the methods of Thompson (1942) in which some system of coordinates is established on the original form and allowed to distort itself as the lines follow the elements that they intersect. In such construction it is a more or less general practice to start with a set of right angled rectilinear coordinates. This procedure will yield all the usual data from such a series, but in the present case, instead of applying the simple Cartesian system, it was found to be easier to follow the transformations by the use of a system of polar coordinates with its origin at the center of the eye. The reasons for this are manifest. In the generalized fish skull the surface bones are arranged in a series of essentially concentric elements about the eye. This is obvious from Text-figure 1a. This same skull is shown in Text-figure 2a with such a grid of polar coordinates superimposed upon it.. These coordinates are purely arbitrary in dimension and any other distances between the lines would have been just as suitable. Following these through to La Cueva Chica blind fish, Text-figure 2b, the regularity of the changing elements in their basic topography is evident and this stage is clearly intermediate between the river fish and the further advanced Cueva de los Sabinos fish, Text-figure 2c. From even a cursory examination it at once becomes evident that the whole skull, as a unit, is shifting and what would at first seem to be capricious changes in bone shapes and sizes are actually mandatory on each element if it is not to do violence to some master plan that controls the architectural changes.

It is curious that the radial ordinates in all still find a common center in the orbit and it is possibly more than accidental that the central circular ordinate becomes more or less bean-shaped, with the concave side uppermost, which is in agreement with the shape that the reduced eye capsule approaches. It should also be noted that it is only by treating the so_3 in its three parts as a unit that the integrity of the regularity of the intersecting coordinates can be retained. This could be taken to suggest that this increase in number is truly due to a process of fragmentation. Likewise in Text-figure 2c, where so_3 is again a single bone, if the other two continued to exist and were treated as before, as a unit, the regularity of the superimposed grid would be destroyed. In a similar manner the other cranial elements could be discussed, as all subscribe to this general proposition. That is, if they were disposed in any other way, independently of the rest, and there is adequate room from such changes, a smooth flowing grid of parallel or regularly diverging lines would not fit. For example, the greatly expanding supraorbital and the contracting frontal would seem to have no independent reason and the two could have remained very much more as they were and still jointly cover the same space, but as is clear from the figures



TEXT-FIG. 2. Transformation of polar coordinates centered in eye. **A.** Normal-eyed river fish. **B.** Fully blind specimen from La Cueva Chica. **C.** Cueva de los Sabinos fish.

they do change their relative sizes, as if merely to meet the inscribed coordinates in a regular manner.

If it is objected that there are actually small divergencies in each of the two distortions of the initial grid it must be borne in mind that such divergencies can be of two sorts: partly organic irregularities and partly artifacts due either to the difficulties involved in handling these small skulls or to the ineptness of the draughtsman. The remarkable part of the constructions seems to the author to be, not small discrepancies but rather that there is such a large amount of profound agreement between the distorted grids and the skull elements themselves. It must be borne in mind in this connection that similar constructions have been made between related species which had all their organs intact and merely varied in dimension. When, in a case such as the present, a dominating organ is merely subtracted, it would seem to be of more than passing interest that the remaining parts do show such a fundamentally simple basic plan in reconstituting themselves. It also goes far to indicate the nature of the influence of the eye on the whole pattern of development of the fish skull.

In making these constructions the actual method employed was to point off, item by item, the intersections of a given line corresponding to the grid placed on the normal-eyed skull. Then a line was drawn through these points freehand as one might draw such a curve from any biological data. Thus, some of the points fall exactly on the line and others scatter slightly to either side of it. It would have been a greater refinement to use some method of curve fitting such as the method of least squares, but the limitations of accuracy of the basic material clearly do not warrant such elaborate treatment. When these lines were inked in with the aid of draughtsman's curves it was discovered that the radial ordinates, whatever the nature of their curvature, were all clearly not logarithmic, but that the concentric ordinates partook of this character to a very large degree. That is to say, it was found that for the latter the so-called draughtsman's "Logarithmic spiral curve" fitted these freehand curves perfectly for much of their length while for the radials it was necessary to employ the so-called "Irregular or French curves" to obtain a fit.

Those portions of the concentric ordinates anterior to the diagonal passing through the coracoid, so$_3$ and supraorbital, maintained their logarithmic feature almost completely. Those posterior to this line took on a distortion, increasingly so as they approached the opposite diagonal, passing through the mandible, so$_2$, so$_5$ and the scale bone. Nevertheless these curves were nearly all drawn by means of the logarithmic spiral.

All this would seem to indicate the very great influence of the eye on the whole architectural plan of the skull. It is interesting to compare this essentially exponential rearrangement of a skull with its central element removed with the logarithmic growth forms of mollusc shells discussed at length by Thompson (1942). The fact that in a structure as complicated as a fish skull such logarithmic elements are clearly present, as have been so simply and elegantly demonstrated in a clam, is evidently due to the fundamental nature of growth, which in an intricate structure becomes involved and complex but does not obliterate the basic regularities inherent in organic development.

If we look upon this polar grid as a field-of-force diagram in which the concentric ordinates represent equipotential lines, the eyed fish would seem to have its elements disposed very much in accordance with the grid centered in the eye as arbitrarily laid down. A notable exception to this is the disposition of the supraoccipital, which has a strong radial trend. In the other two fishes it will be noted that the greatest distortion of these grids is close to, but not identical with, the seemingly radial trend of the supraoccipital. The grids conceived as fields of force change in such a way as to suggest that there is only one pole of any significant magnitude in the area covered by the grids, namely, that centered in the eye. If another were present it would be expected to lead to some dumbbell-like curves, which are clearly absent. On this basis the curious outward extension through the scale bone becomes explainable on the basis that it is due to another field of influence lying outside of the area of the limits of the grid and which if extended might produce such dumbbell-shaped figure characteristic of a bipolar field. The only evident structure that this diagonal and the "points" of the concentric ordinates are directed toward is the base of the dorsal fin, which, in advance, would be expected to exert such an influence. This is not reflected in the original "monopolar" field which is completely arbitrary, but shows good agreement with the circular disposition of the skull elements, except in the supraoccipital area where they appear to be radial in arrangement as previously noted. Clearly, then, when these circles distort with the shifting skull elements, they become affected by any other influence, such as that of a second polar field, which is ignored by the very nature of the original grid. This is actually what has evidently happened in these transformations. It thus may not be far from the truth to say that these diagrams indicate the almost complete dominance of the eye except as modified by a dorso-caudad influence probably rooted in the dorsal fin.

Considering the concentric circles of Text-figure 2a not as polar coordinates, nor as equipotential lines of force but as simple geometrical figures expressible in formulæ on ordinary graphic treatment, it is possible to express the first by the equation

$$(x - p)^2 + y^2 = e^2x^2$$

This, of course, is the basic formula for conic sections, of which the circle is merely a special case, and which is more simply expressed as

$$\frac{X^2}{M^2} + \frac{Y^2}{m^2} = 1$$

in which M = ½ the major axis and m = ½ the minor axis. The other two grids should be expressible by some exponential expansion of this expression. Then the difference between the three expressions should yield a mathematical measure of the basic nature of these differences. Obviously with the present case the labor involved would hardly justify making the involved calculations necessary and this is mentioned merely to indicate an approach that might have considerable utility in other but similar connections.

Lest it be thought that some artifact has been introduced by centering polar coordinates in the eye, that is, on a structure in which the elements are obviously arranged more or less concentrically, other constructions have been made. One on an orthogonal basis shows essentially the same thing, as it necessarily must, but in not so clear a fashion; it consists of both horizontal and vertical ordinates approaching each other in the eye region and suffering considerable distortion in the temporal region; its verticals and horizontals in this region both bend toward the dorsal fin. Another construction on polar coordinates centered in the scale bone shows approach of the concentric ordinates in the eye region while three of the radials, the anterior horizontal, lower vertical and the included diagonal, approach each other in the eye region and pass through the scale bone and with slight angular divergence also point to the dorsal fin region.

Instead of discussing the matter in terms of centers of influence which was based primarily not on these constructions but on the long recognized concentric arrangements of the surface bones of the head it might be more appropriate to consider the matter in terms of lines of strain; the large obvious one in this case being that which runs diagonally upward and back from the mandible through the eye and occipital region. Since the skull is under various strains from muscular attachments it is perhaps to be expected that such a distortion line should appear in a direction involving both the powerful mandibular musculature and to the point of attachment of the occipital condyle which involve also the whole locomotor body musculature. Such considerations, however, would carry us beyond the province of this communication.

A still further analysis can be made by these methods for the purpose of trying to understand their full implications. If any sets of the constructions be drawn superimposed on one paper, then the homologous intersecting ordinates may be connected by lines of varying length with an arrow at their forward end indicating direction of travel of this point on the transforming skull. Very complicated diagrams result that do not look unlike weather maps with their arrows of wind direction, but in which the length of the arrow indicates the proportional distance of travel. By combining visually each of the three sets of diagrams, using different ordinates, it becomes apparent that all show the same features in different terms; this agrees nicely with what has already been set forth. But again this is not the place for extended discussions of such matters.

As further evidence of the similarity of these constructions to those of fields of force it may be mentioned that Hartridge (1920) and Ponder (1925a and b) applied the equipotential curves of Cayley, developed to describe magnetic fields, to the shapes of erythrocytes, and Breder (1943a) discussed them in connection with the shapes of fish eggs. With the information at hand, based on the construction of the polar grid, it would be of interest to recalculate the whole matter on a basis not of equally spaced concentric lines but on the locus of the equipotential curves of Cayley; but this would clearly carry us out of the bounds of the present contribution and no further into an understanding of the eye itself.

Obviously, what has been dealt with here is a projection of one of the three dimensions and for a rigorous analysis all should be considered, just as the equipotential curves of Cayley are descriptive of surfaces and not of lines on a plane. Breder (1943a) discusses these relations in connection with fish eggs and Thompson (1942) gives an extended dissertation on the whole matter.

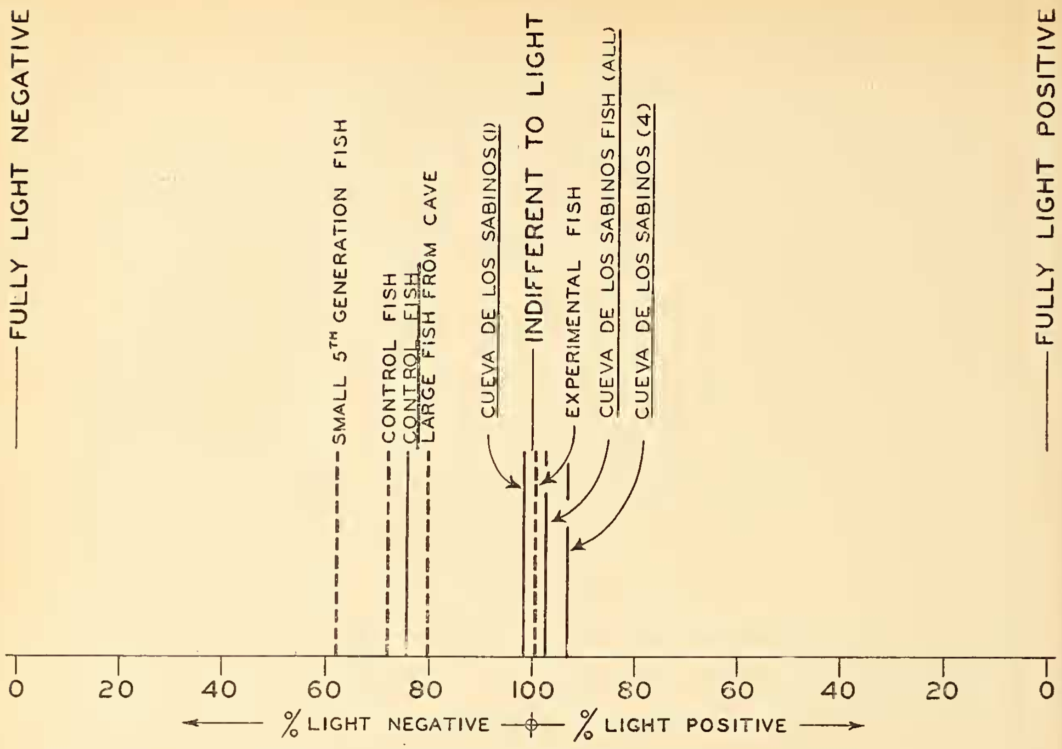
The preceding discussion has centered on the dermal elements of the skull and suffice to indicate the essential regularity of the modifications. No attempt has been made to analyze the rearrangements of the chondrocranial elements which among other things would practically demand a difficult three-dimensional treatment. It was evident from the sections however, that the bones forming the eye socket underwent extensive modification. These did not close in, as might be thought, but became thinner and lost their solid attachment to the brain case, to some extent actually increasing the tissue-débris-filled eye socket in the Cueva de los Sabinos fish.

Experiments on Light Reactions.

In order to determine the extent of light sensitivity in the Cueva de los Sabinos fish, an experimental approach was made similar to that employed by Breder & Gresser (1941a and c). For this purpose two troughs were prepared with one end covered and the other under the influence of a 25-watt light. They each measured thirty-nine by seventeen and one-quarter inches and were filled with water to the depth of one and one-half inches. Thus there were two equal compartments each nineteen and one-half by seventeen and one-quarter inches and identical except that one was illuminated and the other under a solid cover one-half inch over the water's surface.

At five-second intervals the positions of the fishes were noted in reference to which compartment they occupied. From this work the data of Table I were compiled and directly compare to the earlier work on the other forms. It is clearly evident from this Table that the fish from Cueva de los Sabinos show no clear reactions to light under the conditions of the experiments, as compared with the earlier studies or as compared with the La Cueva Chica specimen used as a control against the Cueva de los Sabinos material. Because of the agreement of the latter with the more extensive earlier studies, it was possible to reduce the number of tests, as all the earlier work can be considered as a control for the present experiments.

Text-figure 3 shows these results in graphic fashion and compares the present data with that of the earlier work. This is indicated by dotted lines. It will be seen that the present control fish, La Cueva Chica stock, gave readings of between 60 and 80 per cent. light negativeness in terms of random expectation. As pointed out by Breder & Gresser (1941a), the smaller of these approach 60 per cent. of expectation while the largest approach 80



TEXT-FIG. 3. Comparison between light reactions in fishes from La Cueva Chica and from Cueva de los Sabinos, shown by solid lines, and between La Cueva Chica specimens with and without optic capsule, shown by dotted lines, from Breder & Gresser (1941b). New data indicated by underlining. All expressed in terms of expectancy of random movement. See text for full explanation.

per cent., the reason clearly being due to the greater absolute mass of tissue overlying the blind but light-sensitive capsule. Its removal, as they showed, places the fish close to 100 per cent. of expectation, as indicated in Text-figure 3. It is close to this point that all the readings on the Cueva de los Sabinos material is located. This was, of course, to be expected since it has been shown that these fish lack all remnants of retinal structure and there is no connecting optic nerve. They are thus normally comparable to the condition produced in the La Cueva Chica material by operation.

The La Cueva Chica stock is thus separated from that from Cueva de los Sabinos as well as from operates by a range of nearly 20 per cent. as measured by this system of notation, checking perfectly with what might be deduced from the morphology of the situation.

DISCUSSION.

Although in all the experiments on light reactions in this and the two earlier papers care was exercised to avoid thermal differences in the light and dark chamber, the direct effects of radiant energy of course could not be eliminated. Although all examples with some light sensitivity reacted negatively to light, see Breder & Gresser (1941a and b), it will be noted that those forms without an optic nerve or with the capsule removed show a mean value slightly on the positive side. Since in all there have been 72 such experiments made, the present data and that of Breder & Gresser (1941b), this may well indicate a significant difference. Expressed another way, all but one of the sets of experiments were somewhat over 100 per cent. on the scale adopted. It is suggested that this may be reflecting a slight positive bias on the part of these apparently light-indifferent fish to accept the warmth of the radiant heat of the light bulb, perhaps very much as a blind man can detect the edge of a shadow if the sun is bright, but on a much finer scale of discrimination. Since these fish move readily into the direction of warmth, as has been indicated before, this effect is surely to be expected. To measure this in any great degree of refinement a number of difficult obstacles present themselves and the present methods are not delicate enough to certainly determine it. Such an attempt has not been made, for with other facts already at hand it seems to be not of sufficient significance in present connections.

Scharrer (1928) has shown that blinded *Phoxinus laevis* are light sensitive. This sensitivity he found located directly in the midbrain, made possible, at least, by the thin and not completely opaque overlying structures. He concluded that possible skin sensitivity was definitely not involved. It might be that the effect above considered is actually a measure of a similar condition in these fishes. Experiments along the line of those conducted by Scharrer would have to be undertaken in order to determine these effects, although it does not seem that he eliminated the possible effect of radiant heat, as above considered, from his experiments.

In connection with this it should be noted that very few fishes have been unequivocally shown to possess integumentary photosensitivity. It is evidently present in (*Chologaster*) *Forbesella*, Eigenmann (1909), and in *Amblyopsis spelaeus* DeKay, Eigenmann (1909), Parker (1909a) and Payne (1907). In addition to these fishes proper it is present in larval *Petromyzon* (or *Lethenteron*) Parker (1909a). Although absent in *Amphioxus*, photosensitive cells are located in the nerve tube and exposed by the transparency of the creature, Boeke (1902) and Parker (1908a and b).

A variety of species, *Fundulus heteroclitus* (Linnaeus), Long (1904), Parker (1909a and b), *Fundulus majalis* (Walbaum), Long (1904), *Mustelus canis* (Mitchill), *Anguilla rostrata* (LeSueur), *Stenotomus chrysops* (Linnaeus), *Tautogolabrus adspersus* (Walbaum), *Tautoga onitis* (Linnaeus), *Chilomycterus schoepfi* (Walbaum), *Opsanus tau* (Linnaeus) and *Microgadus tomcod* (Walbaum), Parker (1909b) were shown to have no such sensitivity. It would thus seem that dermal photosensitivity is largely absent in fishes, only the Amblyopsidae having had such demonstrated. Other kinds of such sensitivity, as in *Phoxinus*, would seem to be incidental to the translucency of structures overlying the central nervous system.

Although the La Cueva Chica material will avoid light except if it is overridden by sufficiently large thermal or other differences, it is evident that the Cueva de los Sabinos fish indicate no such negative reactions to light. Thus it follows that while the first are probably held in their cave by this means, the latter are not protected from blundering into a surely fatal environment by any such mechanism. Until much more is known about the geography of Cueva de los Sabinos we can only speculate as to whether these fish are prevented from entering outside waters by physical barriers or whether there is a continual drain off of that population. Although direct tests have not been made it is to be expected that the fish from Cueva de los Sabinos will be found to react to current and water temperature in a manner essentially identical with those of the fishes from La Cueva Chica and eyed river fish. The essential similarity of their gross reactions as well as minor differences in behavior in reference to other senses are discussed by Breder & Rasquin (1943).

It is possible that physiological methods of greater refinement could show light sensitivity on a "micrometric" basis by some modification of the methods of Kurodo (1932), who showed by a kymograph trace that certain fishes gave an immediate respiratory response to various chemical stimulæ. Such a method was found inadequate to the peculiarities of these fishes as is reported by Breder & Rasquin (1943).

As with the development of chemical sensory changes discussed by the above, the eye structure, the skull architecture and behavior of the Cueva de los Sabinos stock as reported here also suggest that these fish are a further development of the conditions found in La Cueva Chica material rather than that the two are independent developments. Whether or not the present La Cueva Chica material should be looked upon as "hybrids" between some small and isolated group of Cueva de los Sabinos fish and the Rio Tampaon stock made possible by a new contact the present studies do little to illuminate.

Hatch (1941) considers that degeneration occurs in caves, because in the absence of selection, mutations of various kinds can survive and that degeneration follows because most mutations are those of loss. Walls (1942) holds similar views, writing as follows:

"Just how the eyes of any blind fish species were led to disappear, we cannot say. An old idea was that where the eye had become useless, there was a positive incentive for eliminating the organ, since this would save energy both in adulthood and—especially—during growth. This notion seems ridiculous nowadays, for the proportion of a growing animal's food-intake which goes to enlarge the eye is negligible. Most of the energy released from food goes for motor and secretory activity, and only a very small part of the food is converted into new protoplasm. Nor does the disappearance of an eye leave a hole in the head—its volume is occupied by tissues (mainly muscle) which consume just as much energy as the eye had done.

"Though a normal eye is excess baggage to a cavernicolous or limicolous fish, there appears to be no urgent reason why he should get rid of it. Useless organs do not always promptly disappear simply because they have become useless—as witness the human appendix, coccyx, platysma, tonsils, wisdom teeth, *et al.* We are left to suppose that in the immediate outside ancestors of most cave species the eye was 'trying' to disappear anyway, but was prevented from doing so, by natural selection, because it was useful and necessary. The usefulness once removed by the assumption of cavernicolous life, the inherent tendency for the eye to shrink was allowed to express itself, even onto the logical end-result—complete loss.

"This explanation does not tax the imagination of ichthyologists as severely as one might think. In many open-water fish species, reduced-eyed individuals appear as soon as the food supply is made abundant and predatory enemies are removed. Lack of competition then permits the full development of individuals which, since their germ-plasm has undergone 'mutations of loss,' would formerly have been suppressed by starvation or capture. Loss-mutations are known particularly to affect the more complex organs of vertebrates, such as the eye. A species or family in which such mutations occur with especial frequency has of course no advantage, over others, in any attempt to become adjusted to a habitat in which illumination is reduced or absent. But if a group which throws loss-mutations also produces an unusual number of other trial-and-error modifications (as seems likely), then such a group might readily evolve the dermal sense organs, barbels or what-not required to cope with a dim-light environment. Once adapted to dim-light existence, such a group would actually be better off in a cave, if it happened to find one, than outside where there were predators to be dodged. And once inside the cave for good, a rapidly-mutating species would inevitably lose what remained of its eyes, though without being under any positive necessity of doing so."

Pike (1943a and b) would refer such degeneration to thermodynamic irreversibility and states his interesting views as follows:

"Confusion has arisen concerning certain processes which have been called reversible, in living organisms. For four decades, biologists have searched for so-called reversible processes comparable to the so-called reversible processes of general chemistry. The object was to disprove the existence of supposed vital characteristics of living organisms. A number of these processes have been found, although there has been scepticism concerning their actual reversibility under biological conditions. In these four decades, we have come to recognize more clearly that, in inorganic nature, processes which are not strictly mechanical are irreversible, thermodynamically.

"Two costs must be reckoned in non-mechanical processes—that in free energy, and that in entropy. Unless both can be kept at zero when the operation is put through in the reverse direction, the process is irreversible thermodynamically. 'If an irreversible process can occur, it will occur.' (Houstoun). Unless there is some mysterious mechanism in living organisms to forbid irreversible processes, they will occur. Experimentally, we have found many such, but we have never found one which is reversible thermodynamically. To show the existence of reversible processes in living organisms would be the equivalent to a demonstration of vitalism.

"These considerations bear on certain hypotheses of heredity, the transmissibility of the effects of the environment, and the degeneration of specialized tissues in changed environments, some of which hypotheses postulate thermodynamically reversible reactions, or their equivalent in thermodynamic efficiency.

"It has been asserted that degeneration of eyes of cave forms is due (1) solely to chromosomal changes, and (2) to inheritance of the effects of the environment. Since photo-receptors appear only in species which have some time lived in the light, it seems permissible to assume some causal relationship between light and photoreceptors until demonstration of their complete independence.

"The chromosomal hypothesis of degeneration of the eyes of cave forms postulates that the process of heredity will go on for generation after generation, with no dissipation of free energy or gain in entropy, and, hence, be a truly thermodynamically reversible process, or a process of equivalent thermodynamic efficiency, such as is found nowhere else in nature.

"Since darkness is merely the absence of light, and cannot be a form of energy, it can have no positive effect, and can produce nothing. Since it has no positive effect, the effect of darkness could not be transmitted hereditarily.

"The observed result of living in perpetual darkness is what we would expect when organisms experience a failure of the driving force concerned with the development of photoreceptors.

"When the phenomena of recession and degeneration, of use and disuse, in ontogeny and in phylogeny, are regarded from the dynamical point of view, there appears to be some fundamental relationship to their irreversibility, in the thermodynamic sense of irreversibility."

There is clearly no basic conflict between these two views or the view that genes carrying eye defects can be perpetuated in such environments and spread through the population by some such means as expressed by Hubbs (1938) of which Breder (1943b) wrote, "An interesting speculation on the possible mathematics of the genetic reduction of other than blind white forms coupled with repeated separation of small population groups is discussed by Hubbs."

In this connection the interesting report of Ogneff (1911) showed that gold fish kept in darkness up to three years suffered histological degeneration of the retina. He was satisfied that his fish were blind. Unfortunately he says nothing about light sensitivity. The eyed specimens from La Cueva Chica were mentioned by Breder (1943c) as follows: "All fish brought freshly from the cave act like the blind fish in regard to feeding. This has been checked twice, all forms from the cave performing circling movements for food finding for at least a couple of months and then those with structurally good eyes apparently learning the meaning of a retinal image and taking on the feeding habits of the river fish. These forms at all times, from the first, 'jump' at the passage of a shadow, like those with merely an exposed retina." It is proposed to check this material histologically to determine if this inability to find food by visual means had to do with retinal degeneration and later reorganization under the influence of light or on a basis of learning. The work of Ogneff (1911) strongly suggests that the former may be playing a large part in this connection. The nature of such changes in either direction should yield data bearing on the views of Pike (1943a and b).

Summary.

1. The blind characins from Cueva de los Sabinos, San Luis Potosi, Mexico, differ from those of La Cueva Chica, which is about fifteen miles distant, in that the former show a still further structural loss in eye architecture.
2. Nothing is left of the retinal tissue and all that can be found in the socket is a much reduced pigmented cyst which may represent the last of the coroid.
3. The last vestige of a connecting optic nerve is gone.
4. Along with the eye loss has come modification of the skull, involving a closing in of the circumorbital series of bones, and some de-ossification.
5. Great regularity is shown in the rearrangement of the bones of skull with the subtraction of the eye, clearly indicating a reconstitution of the skull as a whole in which the separate elements are without independent action.
6. Experiments with a gradient trough show that these fish are fully indifferent to light as compared with the negative reactions of La Cueva Chica specimens.
7. Current views on the biology of such degenerative changes are discussed.

Table I. Tabulations of Experiments on Light Sensitivity.

Each experiment represents 100 notations at 5-second intervals.

Exp. no.	Type of fish	Number of fish	Observed in light	% of random expectation
1	La Cueva Chica[1]	1	30	60
2	" " "	1	24	48
3	" " "	1	28	56
4	" " "	1	63	126
5	" " "	1	27	54
6	" " "	1	77	154
7	" " "	1	12	24
8	" " "	1	49	94
9	" " "	1	53	106
10	" " "	1	17	34
		Mean	*37.8*	*75.6*
11	Cueva de los Sabinos[2]	1	49	98
12	" " " "	1	63	126
13	" " " "	1	51	102
14	" " " "	1	45	90
15	" " " "	1	80	160
16	" " " "	1	44	88
17	" " " "	1	16	32
18	" " " "	1	17	34
19	" " " "	1	36	72
20	" " " "	1	89	178
		Mean	*49*	*98*
21	Cueva de los Sabinos[3]	4	158	79
22	" " " "	4	156	78
23	" " " "	4	226	113
24	" " " "	4	223	111.5
25	" " " "	4	240	120
26	" " " "	4	257	128.5
27	" " " "	4	273	136.5
28	" " " "	4	233	116.5
29	" " " "	4	212	106
30	" " " "	4	161	80.6
		Mean	*213.9*	*106.9+*
		Mean of Exps.	11 to 30	102.5—

[1] This fish seventh generation of tank-reared stock, 49 mm. in standard length.

[2] This fish from Cueva de los Sabinos, 46 mm. in standard length.

[3] These fish from Cueva de los Sabinos, between 46 and 49 mm. in standard length.

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EXPLANATION OF THE PLATE.

PLATE I.

Sections through the left orbit of specimen from Cueva de los Sabinos.

FIG. 1. The central body represents the cartilaginous capsule within which is a pigmented cyst surrounded by loose connective tissue. Magnification 80 ×.

FIG. 2. A slightly more posterior section showing the medial wall of the capsule to be here composed of connective tissue. At about the center of the connective tissue portion is a mass made up of muscle and possibly an atrophic nerve. Magnification 62 ×.